

ORIENTATION BEHAVIOR OF THE SLAVE-MAKING ANT *Polyergus breviceps* IN AN OAK-WOODLAND HABITAT

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Abstract.—The orientation behavior of *Polyergus breviceps* was studied in an oak-juniper woodland in southeastern Arizona. Target colonies of *Formica gnava* were scattered in all compass directions around the *Polyergus* nests. Tests conducted at the front of the slave-raid swarm showed that optical stimuli, especially polarized light, are the principal cues for worker orientation. There was no evidence that the ants were following a chemical trail previously deposited by a successful scout. After the slave raid, workers of *Polyergus* returned to their home nest by responding simultaneously to optical cues and to a chemical trail that they had deposited during the outbound raid. Although it is possible that naive individuals, scouting for the first time, may indeed rely more heavily on a chemical trail, all evidence to date indicates that experienced scouts utilize optical orientation.

The parasitic formicine ant genus *Polyergus* consists of four species, all characterized by a worker caste that is specialized for conducting group raids on colonies of the related genus *Formica* (Yasuno, 1964; Talbot, 1967; Dobrzńska, 1978; Topoff et al., 1984). Although up to 75% of the raided pupae are eaten (Kwait and Topoff, 1984), those that are reared through eclosion subsequently assume the chores of foraging, brood-rearing and nest maintenance for the mixed-species colony.

Compared with other groups of ants, relatively little is known about the processes of communication and orientation utilized by scouts and raiders during the slave raids. In studies of *Polyergus lucidus*, Talbot (1967) and Marlin (1969) emphasized chemical communication, and concluded that individual scouts deposit a trail from the target *Formica* colony back to their home nest. In a recent study of the western species *P. breviceps* in Arizona (Topoff et al., 1984), we discovered that scouts utilize optical orientation when returning from colonies of *Formica gnava* to their home nest, and when leading nestmates on the slave raid. During the raid, both scout and raiders deposit a chemical trail. After the raid all individuals return by a combination of optical orientation and following the chemical trail deposited on the outbound trip.

The reliance of *P. breviceps* scouts on optical cues in our study may have been enhanced by the unique ecology of our desert study site. All *Formica* nests in this area were located to the south of the experimental *Polyergus* colony, in the narrow riparian zone created by Cave Creek. As a result, practically all scouting and slave

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raiding took place in the same general direction. Under these conditions, experienced scouts may require only optical cues for successful orientation.

In this paper, we report the results of comparable orientation studies, conducted in an oak-juniper habitat where target *Formica* colonies are scattered in all compass directions around *Polyergus* nests. The goal of the study was to determine whether the role of chemical orientation would be increased in this more "complex" habitat.

MATERIALS AND METHODS

Studies of orientation were conducted at the Southwestern Research Station of The American Museum of Natural History, located 5 km west of Portal, Arizona. At an altitude of 1,646 m, the dominant vegetation consists of Arizona oak, alligator juniper, and Chihuahua pine. Two colonies of *P. breviceps* were used for the study, during July and August of 1983.

To elucidate the stimuli utilized by *Polyergus* for orientation during scouting and raiding, a series of tests was performed as the ants moved to (outbound) and from (inbound) target colonies of *Formica gnava*. All studies were conducted between 1600 and 1730 hours (MST), as the ants crossed a predetermined, 2-m wide test area that was relatively devoid of trees. For the inbound test series, observations of the ants' behavior were made after a slave raid, when the number of returning ants crossing the test area was at or near its peak. As indices of the ants' "confusion," we recorded: (1) the number of turns greater than 45° made by test individuals; and (2) the direction in which the ants were oriented (with respect to their home nest) at the end of the test interval. This bearing used 0° as the homeward direction, which was assigned if the ant's posterior-to-anterior axis pointed with a range of 45° to the left or right of the 0° direction. The 90°, 180°, and 270° positions were similarly designated. Each of 15 ants was observed for 30 s, starting when the subject first contacted the test area. For the inbound test series, each of the following conditions was conducted two times:

(a) Control: To provide baseline data for subsequent comparison, two sets of observations were made on returning ants that were not subject to any manipulation.

(b) Diffused sun-normal sky: After the outbound slave-raid swarm had crossed the road, a wooden frame (2.5 m²) covered with waxed paper was positioned over the test area at a 45° angle, so that returning ants could not see the sun directly (which was low in the western sky in the afternoon). The frame was positioned with its upper end sufficiently to the west so that the sky directly above the returning ants was fully visible.

(c) Diffused sun and sky: In this test condition the waxed paper frame was suspended horizontally across the test area (1.5 m above the ground), thus diffusing the light from both the sun and the sky overhead.

(d) No trail: After the outbound column had crossed the test area, we used garden hoes to remove the top layer of soil (and therefore any chemical trail that the ants might have deposited on the outbound raid).

A second identical series of tests was conducted on outbound *Polyergus* workers, when the front of the raiding swarm first entered the test area. In this outbound series, the 0° bearing was assigned if the ants' posterior-to-anterior axis pointed away from the home nest.

Table 1. Mean number of turns and chi square (χ^2) distributions for 30 individuals of *Polyergus breviceps* during slave raid (outbound) and return (inbound) trip.

Test condition	Inbound			Outbound		
	Mean no. turns	χ^2	<i>P</i>	Mean no. turns	χ^2	<i>P</i>
Control	0.9	30.6	<0.01	1.4	18.7	<0.01
Diffused sun-normal sky	1.1	30.5	<0.01	1.9	24.7	<0.01
Diffused sun and sky	9.3	0.7	NS	10.6	1.3	NS
No trail	8.0	1.3	NS	1.2	24.7	<0.01

NS = not significant.

RESULTS

The orientation behavior of *Polyergus* in the two test series is represented in Table 1. All values in the table were calculated by combining the data for the two replicates of each test condition. Comparisons of turns were based upon an analysis of variance. Because the analysis showed a significant effect for conditions [$F(7, 112) = 53.3$, and $P < 0.01$], we utilized a Tukey test of multiple comparisons to determine significant differences among condition means (with $P < 0.01$). A chi square test was utilized to indicate whether the number of ants moving toward each of the four compass directions represented a random distribution.

In the unmanipulated control condition (inbound series), the mean number of turns was 0.9 and 87% of the returning ants were moving in the homeward direction at the end of the observation period. This clearly represents a non-random distribution with respect to the four possible directions ($\chi^2 = 30.6$ in Table 1). When the ants could only see a diffused sun, but a normal sky directly overhead, their orientation behavior was essentially unchanged. However, when the waxed-paper frame was placed horizontally over the returning ants (so that the light from both the sun and sky were diffused), the efficiency of their homing behavior decreased markedly. The mean number of turns was significantly greater than that of the control and "diffused sun-normal sky" conditions, and the chi square test showed that the ants were moving randomly. Finally, removal of the chemical trail, even though the ants' view of the sun and sky was not obstructed, had an equally disorienting affect on their homing behavior. The mean number of turns, although significantly greater than that of the control and the "diffused sun-normal sky" conditions, was not significantly different from that of the "diffused sun and sky" condition.

In the outbound test series, conducted when the slave raiders were en route to the target *Formica* colony, the first condition again served as a control. Our observations began when the front of the raid swarm entered the test area. In the control condition, the mean number of turns made by the 30 observed raiders was 1.4, and the ants were oriented toward the target nest ($\chi^2 = 18.7$). In the "diffused sun-normal sky" condition, the orientation of the advancing slave raiders was again correct. In the "diffused sun and sky" condition, however, the advancing raid came to an abrupt halt as soon as the ant swarm entered the area of testing that was covered by the waxed-paper frame. The mean number of turns was significantly greater than that

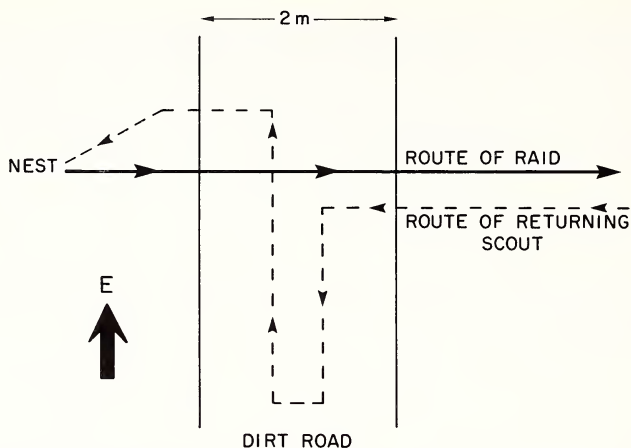


Fig. 1. Path of returning scout (broken line) whose route was artificially altered, compared with route of slave raid (solid line) subsequently led by the same scout.

of the first two test conditions, and the ants were moving randomly over the four compass directions ($\chi^2 = 1.3$). When the haphazard movements of the *Polyergus* brought them beyond the boundaries of the waxed-paper frame, they immediately resumed their forward direction. In the last experimental condition, when the advancing ants crossed the test area that had its top layer of soil removed prior to raid onset, the ants' behavior was not significantly different from that of the control.

An additional manipulation further demonstrated the ants' reliance on optical cues. It was conducted during a slave raid towards a colony of *Formica* located 40 m to the south. Prior to raid onset, an outbound scout was marked (on its gaster) with fluorescent powder. When it returned to its home nest, we used a 1.5-m long sheet of plywood to divert its path (Fig. 1). The scout was forced to change direction twice (2 m to the west, followed by 3 m to the east) before resuming its homeward (north) route. Despite this displacement, the scout promptly led a successful slave raid along a straight course to the south.

DISCUSSION

The results of this study of in the oak-juniper woodland are consistent with those from our previous research in the desert habitat (Topoff et al., in press). Thus, although colonies of *Formica gnava* were scattered in all compass directions, the tests in the outbound series showed that *Polyergus* orientation at the raiding front is not based upon chemical cues. Although we did not mark individual ants, our previous study with marked scouts (Topoff et al., in press) showed that most raids are indeed initiated and led by a single scout. In addition, although we have not analyzed the ants' ability to utilize visual landmarks or canopy outlines (Hölldobler, 1980), their severe disorientation under the waxed-paper (which diffuses light) suggests that polarized light may be the principal stimulus (Wehner, 1969). Our previous desert study also showed

that the position of the sun is an additional cue, because *Polyergus* workers could be reversed by "displacing" the sun's direction with a mirror.

Results from the inbound test series indicate that workers of *Polyergus* returning from a raid orient by responding simultaneously to optical cues and to a chemical trail that they deposited on the outbound slave raid. Such simultaneous reliance on diverse sensory processes is well documented for many ants, including the genera *Neivamyrmex* (Topoff and Lawson, 1979; Topoff et al., 1980) and *Pogonomyrmex* (Hölldobler, 1976)

Perhaps the most obvious discrepancy between our findings and those from studies of the eastern species *P. lucidus* (e.g., Talbot, 1967; Marlin, 1969) is our conclusion that *P. breviceps* scouts rely on optical rather than chemical stimuli for orientation. It is of course possible that *Polyergus lucidus* and *P. breviceps* scouts utilize different cues. A more likely explanation for the discrepancy, however, is that studies of *P. lucidus* have only demonstrated orientation over artificially-deposited chemical trails. In none of these studies was the role of optical orientation even considered. We favor the optical orientation hypothesis because it is consistent with the method by which *Polyergus* slave-raid swarms typically find target nests of *Formica*. In studies conducted with marked ants (Kwait and Topoff, in press; Topoff et al., in press) it was observed that the original scout is frequently *not* the individual that relocates the target colony. The scout runs intermittently at the head of the raid swarm, and usually leads the raiders only to the general area of the *Formica* nest. She then stops advancing (and presumably also stops depositing the recruitment trail). When this occurs, the *Polyergus* workers (which may number more than 2,000 individuals) also cease advancing, and fan out over a roughly circular area up to 3 m in diameter. Because any *Polyergus* worker that encounters the *Formica* colony can recruit nestmates, the scout need not relocate the target nest with pinpoint accuracy. The adaptive value of utilizing optical cues rather than a chemical trail can be appreciated by considering that target *Formica* nests may be located up to 100 m from the *Polyergus* colony, and that a scout may require more than 1 hr to make the round trip. As a result, a chemical trail deposited by a single scout over such a long distance could easily be disrupted by rain, wind-swept leaf litter, or animal traffic.

Despite the findings from our studies of *Polyergus* orientation, there is one condition in which it might be more adaptive for scouts to rely on a chemical trail. We have previously determined for *P. lucidus* (Kwait and Topoff, in press) that workers do not become scouts until the second season after their eclosion. In the pattern of temporal polyethism that exists for *Polyergus*, workers progress from inside-the-nest activities to preraid circling to scouting. It is thus quite possible that individuals scouting for the first time may deposit a chemical trail from the target *Formica* colony back to their home nest. As they become more experienced, optical cues may then replace the chemical trail. This would be similar to the temporal change in orientation cues described by Henquell and Abdi (1981) for *Formica polyctena*. In conclusion, as Hölldobler (1980) correctly noted, many social insects have a hierarchy of available cues for orientation (and undoubtedly also for communication). Which cues are utilized, and in what combinations, depends upon many factors, including the species' sensory capabilities, social context, stimulus availability, and the age and experience of the individuals.

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